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Behavior of the female beaugregory damselfish, Stegastes leucostictus

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Table of Contents

Abstract

In the territorial, polygynous beaugregory damselfish, females distribute themselves non-randomly such that larger individuals are surrounded by more males. This distribution suggests that large females have access to more mates within a given traveling distance than small females. Aggression between females suggests that they may interfere and influence others' mate choices. Females appear to copy the mate preferences of other females by mating with males who are already fathering eggs. Other investigated factors influencing female choice may be male habitat quality and/or male behavioral traits, such as courtship and aggression. Females visit and reject many males, demonstrating their capability to assess and evaluate perspective mates. In addition, males may also evaluate females, as they preferentially court larger females. Both sexes appear to participate in mate selection.

Introduction

In polygynous territorial systems, only a small portion of the reproductively mature males mate. While the biased reproductive success among males has been correlated to many different male characters such as size (Howard, 1978; Bisazza and Marconato, 1988; Côte and Hunte, 1989), color (Gronell, 1989), courtship intensity (Weatherhead and Robertson, 1977; Schmale, 1981; Knapp and Warner, 1991), and the quality of their territories/resources (e.g., nest quality (Sargent, 1982; Kodric-Brown, 1983; Hoelzer, 1990) and food availability (Gottlander, 1987)), few studies have described how females choose among males. In lek-breeding birds and mammals, where males defend non-resource based areas, females meander through the display area interacting with several males (Dale et al, 1990; Petrie et al, 1991). Sometimes females make several visits to the lek before making their final mating choice(s) (Andersson, 1992). During these visits, females are assumed to be assessing the males.

In polygynous territorial systems, it is unclear how females evaluate more widely spaced males. Females, however, have been observed "visiting" territorial males (Gronell, 1989; Hoelzer, 1990). In comparison to the aggressive behavior of territorial males, there is little information on female behavior in such polygynous systems (Clutton-Brock, 1988).

Janetos (1980) developed a series of simple theoretical models of how females could choose their mates: 1) mate with any random male, 2) mate only with a male who exceeds some threshold value, 3) mate with a male that is close to or better than the average (one-step decision process), and 4) mate with the best of a given number of males encountered (best-of-N strategy). Given the

skewed reproductive success among males in polygynous systems, we assume that females are not randomly mating, but are using one of the comparison methods. Field studies (Petrie et al, 1991; Bensch and Hasselquist, 1992) have identified evidence supporting both the "one-step decision" process (model 3) and the "best-of-N" strategy (model 4) in a territorial and in a lek-breeding bird. In addition, a simple computer simulation has reproduced the skewed reproductive success among males if females sequentially compare two males at a time and mate only with the second male if he is better than the first (Brown, 1981). The paucity of field data on female behavior makes it difficult to evaluate these models.

Here I consider the mate assessment process of the female beaugregory damselfish, Stegastes leucostictus. This pomacentrid is a typical resource-based, territorial, polygynous species. Males have all-purpose territories that are used for food, shelter, and reproduction. Within the territory is a crevice, which serves as an egg deposition site for females. After a female lays her eggs, she leaves the territory. The male provides no direct parental care, but his territorial defense does protect the eggs. A male's crevice is often capable of maintaining several egg clutches at one time. As expected from a polygynous social system, beaugregory males exhibit considerable reproductive variation (Itzkowitz, 1985; Itzkowitz and Makie, 1986). As with most other polygynous vertebrates, very little is known about how female beaugregory damselfish choose males.

The following study investigates: 1) how females are distributed, 2) how females evaluate males, 3) how females influence one another (e.g., copying, where females may prefer to mate with males previously selected by other females), 4) the frequency of courtship, 5) the importance of male habitat

quality to male courtship, and 6) how male behavior affects female mate selection.

Methods

Behavioral observations and experiments were performed between May 16th, 1993 and August 6th, 1993 in Discovery Bay, Jamaica. The shallow backreef averaged 1-3m in depth and consisted of sand and dead coral rubble, with occasional dense blooms of green algae (Chaetomorpha spp.). Beaugregory damselfish were common, but also occurring along the reef in similar habitat were the bicolor damselfish, Stegastes partitus, and the three-spot damselfish, Stegastes planifrons.

I. Distribution

The distribution of males and females was determined by identifying all individuals within a three meter radius of a target adult female. All males and females located around the target female were identified by their behavior. An adult female could only be identified as female when courted by a male. Other characteristics, behavioral and physical, were unreliable in the identification of sex. Likewise, adult males were identified only through their courtship behavior. Each individual's primary crevice, in which most of its' activity was centered, was determined to be within one, two, or three meters from the target female's primary crevice. The relative positions of the males and females were mapped.

Nearest neighbor distances were calculated by measuring the distances separating males and females. A male or female was randomly chosen from the distribution maps and the distances to its nearest male neighbor and its nearest female neighbor measured. The four measurements were: 1) female to nearest male, 2) female to nearest female, 3) male to nearest male, and 4) male to nearest female. Each measurement was independent, as no fish was used as

both a focal individual and a neighbor. Wilcoxon Mann Whitney U Tests were used to determine differences in the distances between males and females.

For a subset of females, size data was also collected. To determine if size was important in how females were distributed among males and other females, Wilcoxon Mann Whitney U tests were performed, using female size (TL) and the number of individuals located around each female as the variables. The female size range was divided such that half the females were "small" and half the females were "large."

II. Individual Female Observations

For long-term identification, 21 adult females, identified by male courtship, were captured with a net, measured (total length, TL, and fork length, FL), and tagged with T-bar monofilament Floy tags placed on the dorsal region of the body. After tagging, the female was returned to the site of capture and followed to determine the location of her primary crevice. After a two day recovery period, these 21 females were observed for 122 fifteen minute periods. Observations were made mostly between 0630h to 0830h and 1400h to 1600h. Preliminary observations revealed that these were the times that most conspecific interaction occurs. During the observations, all modes of behavior, including feeding, territorial defense, home range movements, and courtship/mating, were recorded.

Several measures were used to characterize the distances traveled by each female. The "average distance" was the distance from the female's crevice to where she spent the majority of her time during the fifteen minute observation time. Also measured at the end of each observation time was the furthest distance the female traveled. The average of all the furthest distances traveled

over all the time periods the female was observed yielded the "average furthest" distance and was considered to be the female's territory size. The "furthest overall" distance was the longest distance that each female was ever observed to travel over all the observation periods.

To determine if female size was related to the distance that they traveled from their crevices, Spearman Rank correlation coefficients were calculated using female total length and the distance traveled as factors. To determine if females varied in their feeding activities during the morning and afternoon hours, a parametric ANOVA test was used. A one-way chi-square test was used to determine if females engaged in courtship equally. Because females were not observed for the same number of time periods, five observation periods were randomly selected and totaled to represent the number of courtship events for each female.

III. Nearby Male Territory Manipulation

After five females were observed for a minimum of eight observation periods, artificial spawning sites identical to those used by Itzkowitz and Makie (1986) were given to nearby males. The artificial substrate was made of a 30cm X 30cm plexiglass base with four PVC tubes (length = 10cm, diameter = 7.5cm) bolted to the base in a cross pattern. Previous studies have shown that such artificial spawning sites enhance the reproductive success of their male occupants (Itzkowitz and Makie, 1986; Itzkowitz, 1991). The artificial sites were given to four males within the home range distances of the five focal females, but not to those males that were observed courting those females over the course of at least 150 minutes of observation. The purpose of the manipulation was to determine if interaction between a male and a tagged female could be

induced by changing the male's territory quality. After the artificial substrates were given to the males, the females were observed for at least five more 15 minute periods, each observation period separated by approximately 24 hours.

Possible changes in male and/or female behavior as a result of giving a male a higher quality artificial spawning site could be: 1) the male may court females he previously had never courted or he may intensify courtship (e.g. longer courting time, more often) to previously courted females, 2) the female(s) may be more likely to visit the male's crevice, 3) the female(s) may be more likely to mate with the male, and/or 4) the territory size, movements, or locations of activity of the female(s) may be altered. Thus, regarding the courtship hypothesis, the experiment reveals information only about previously uncourted females.

IV. Group Observations

In an attempt to observe a greater frequency of conspecific behavior, particularly courtship, visiting, and spawning, groups consisting of both males and females were observed. Although the groups were not discrete communities, they were chosen such that many individuals would be visible and all behavior could be reliably recorded. Three groups of eight to twelve individuals, of which at least three were females, were observed for 24 thirty minute periods. Each observation period was separated by approximately 24 hours. Only conspecific behavior was recorded. In addition, any "outside" individuals entering the group area were noted and the locations of their primary crevices relative to the group determined, if possible. After each observation period, each male's crevice was investigated for the presence of eggs. At the end of the study, all individuals in the study groups were captured and measured

(TL and FL). Non-parametric Kruskal Wallace tests determined that the three groups were not significantly different in all behavioral respects (Table 1). Thus, all groups were combined in subsequent non-parametric tests.

V. Copying

Due to the highly skewed nature of male reproductive success in the beaugregory damselfish (Itzkowitz, 1985; Itzkowitz and Makie, 1986), an experiment was performed to determine if female choice was influenced by "copying," a phenomenon where females prefer to mate with males already fathering eggs. The experiment was designed such that the manipulated variable was the presence or absence of eggs, while male behavior was kept constant by randomizing the effects of pre/post-reproductive events. The manipulation made unsuccessful males "successful" and successful males "unsuccessful" by giving and taking away eggs, respectively.

Thirty-six males were given artificial breeding sites (described above) in which the tubes were lined with plastic paper. When any male received a clutch of eggs, the tube containing the eggs was transferred to another male's artificial site that did not contain any eggs. As a control, tubes were also exchanged between the sites of two males that did not receive eggs. A total of 56 egg transfers and 37 control switches were completed. The following morning, all sites were checked for the addition of any new egg clutches. To avoid the complication of multiple egg clutches and egg clutches of varying ages, all eggs involved in a manipulation were scraped away the following morning after data was collected.

Results

I. Distribution

Statistical tests revealed that males were significantly closer to females ($\tilde{x}$ = 1.33m, n = 13) than other males ($\bar{x}$ = 1.62m, n = 14) (Wilcoxon Mann Whitney U Test, n = 27, z = -1.86, p = 0.03) and females were significantly closer to males ($\bar{x}$ = 1.31, n = 21) than other females ($\bar{x}$ = 1.72, n = 21) (Wilcoxon Mann Whitney U Test, n = 42, z = 2.48, p = 0.01) (Table 2).

Female size versus number of males within a 1m radius (Wilcoxon Mann Whitney U Test, n = 6, W_X = 6, p = 0.05) and a 3m radius (n = 6, W_X = 6, p = 0.05) is significant , but not within a 2m radius (n = 6, W_X = 9.5, p = 0.425), although the sample size may not be large enough to reflect the possible effect within 2 meters. Larger females were located closer to more males. Large females averaged 1, 2.3, and 3.7 males, while small females averaged 0, 2, and 1.3 males within 1m, 2m, and 3m, respectively. Female size appears to have no effect on how they distribute themselves among other females (Wilcoxon Mann Whitney U Test, 2m: n = 6, W_X = 8.5, p = 0.275, 3m: n = 6, W_X = 12, p = 0.80).

II. Individual Female Observations

Non-Interactive Behavior

The average distance females traveled was within 1m of their primary crevices ($\bar{x}$ = 0.65m, n = 14) and their average furthest distance was 1.87m (n = 14) away from their primary crevices (Table 3). The furthest a female was observed traveling from her crevice was 12m, when she was found mating with a male defending an artificial breeding site. Considering the "furthest overall" distances traveled, females averaged 3.07m (n = 14) from their crevices. No

significant correlations were found between female size and the average distance (r_s = -0.02, n = 14, p > 0.05), the average furthest distance (r_s = 0.05, n = 14, p > 0.05), or the furthest overall distance (r_s = -0.11, n = 14, p > 0.05) that females traveled.

Females traveled further in the morning (0600h and 1100h; $\bar{x}$ = 3.09m, SE = 0.73, n = 11) than in the afternoon (1100h and 1800h; $\bar{x}$ = 2.30m, SE = 0.33, n = 11) using furthest distances as the measure (Wilcoxon Signed Ranks Test, p = 0.02, n = 11) . No difference was found in their average territory size, as defined by the "average furthest" distances, in the morning versus the afternoon (Wilcoxon Signed Ranks Test, p > 0.05, n = 11) (Table 3).

The feeding frequency of females was found to vary significantly with time of day ($F(1,10) = 143.59$, p < 0.05), averaging 23.25 nips per 15 minutes in the morning (n = 14) and 112.8 nips per 15 minutes in the afternoon (n = 11).

Intrasexual Interactions

Whenever two females encountered one another (i.e. within 25cm), they would either ignore each other or they would be aggressive in the form of chasing or mouth fighting. In the 30.5 hours of individual female observations, 41 female-female encounters were observed. More than three-quarters, 76%, of such encounters resulted in one female chasing the other. In almost all the cases, the intruding female was chased, and occasionally she responded by chasing the resident female back, but still ultimately retreated. In the remaining 13% of the chasing interactions, a female attacked another female that was engaged in courtship and chased her away from the male. Twenty-four percent of all the female-female encounters resulted in the females ignoring one another. In almost all those cases, both females were engaged in feeding.

Intersexual Interactions

Of the 270 female-male encounters (i.e. within 25cm of one another) observed, one or more of the following resulting interactions occurred: 1) the male engaged the female in courtship, 2) the female entered the male's crevice, termed a visiting event, 3) the female mated with the male, 4) the female chased the male, 5) the male chased the female, or 6) the male and female ignored each other (Table 4). Courtship accounted for 71.9% of the interactions. Both modes of intersexual aggression, including the male chasing the female and the female chasing the male, were observed, accounting for approximately 17% of the male-female encounters. One mating event was observed. In this case, the tagged female traveled 10m to the male's crevice and took approximately 10 minutes to deposit her eggs. She visited another male's crevice about halfway through her mating, but did not deposit eggs in the second crevice.

The frequency in which females encountered males did not vary according to time of day ($F(1,10) = 0.81$, $p = 0.39$). It was hypothesized that since females and males encountered each other equally in the morning and afternoon, there would be fewer interactions in the afternoon when females spent more time feeding (See above). This was not the case, however, as eliminating encounters in which the male and female ignored each other from the above test did not change the result ($F(1,10) = 2.604$, $p = 0.13$).

Using frequency of courtship encounters as the variable, a one-way chi-square test revealed that females from this study group engaged in courtship equally ($\sum X^2(11) = 12.84$, $p = 0.30$). Furthermore, female size was not correlated to the amount of courtship each female received ($r_s = -0.003$, $n = 12$, $p > 0.05$).

III. Nearby Male Territory Manipulation

To observe the effects of artificial spawning sites on male and female courtship behavior, sites were given to four males that were located within the home range distance of five females. All four males immediately defended their new sites, but only three received eggs during the ten days of follow-up observations. All three males who obtained eggs in their artificial spawning sites were observed courting their associated females during the ten days of follow-up observations. In one case, the male traveled the 3.5m separating their crevices to court the female. In the other two cases, the female traveled to the male's artificial spawning site and engaged in courtship. One encounter resulted in the female entering the male's spawning site, but did not conclude with egg deposition. Two of the females lost their tags and were eliminated from the experiment.

IV. Group Observations

Courtship

A one-way chi-square test, using frequency of courtship for each individual as the variable, determined that females were not courted equally by males ($\sum X^2(12) = 95.45$, $p < 0.001$). Larger females were courted more ($\bar{x}$ = 19.5 courtship encounters, SE = 2.6) than smaller females ($\bar{x}$ = 7.8 courtship encounters, SE = 0.52, n = 5) (Wilcoxon Mann Whitney U Test, n = 9, W_X = 27.5, $p < 0.05$). These results are notably different from the individual female observations (See above). As females observed individually were significantly smaller than the group females (Wilcoxon Mann Whitney U Test, z = 2.17, n = 22, p = 0.015), size alone may account for this discrepancy.

In addition to females within the observed groups, the males courted other females by traveling to them or courting as the females traveled past. Since, in most cases, it was impossible to note the origin of these additional females, they were placed in a "Miscellaneous Female" category. Including the miscellaneous females as a category, the resulting chi-square (see above) testing for equal courtship among females becomes more significant ($\sum X^2(15) = 330.75$, $p < 0.0001$).

The amount of courtship observed per female per 15 minutes was statistically similar in both the individual female observations and the group female observations (Wilcoxon Mann Whitney U Test, $z = 0.395$, $n = 30$, $p > 0.05$). While females observed individually averaged 1.59 courtship events per 15 minutes (See above, Table 3), females observed in groups averaged 1.39 (SE = 0.133, n = 16) courtship events per female per fifteen minutes.

Males were found to vary significantly in the number of times they courted females, using the number of courtship interactions in which each male engaged as the variable ($\sum X^2(16) = 119.91$, $p < 0.05$). Furthermore, larger males were found to engage in courtship ($\bar{x} = 24.3$ courtship encounters, SE = 1.2) more frequently than small males ($\bar{x} = 12.4$ courtship encounters, SE = 2.4) (Wilcoxon Mann Whitney U Test, $n = 14$, $W_X = 24.5$, $p < 0.05$).

Visiting, Mating, and Aggression

A total of 45 visiting events were observed, of which 13 events (29%) were performed by females within the group and the remainder by females not in the observed focal group. Furthermore, 12 mating events, separate from the visiting events, were observed, 50% of which were by females within the group. All the observed matings took place in the morning hours between 0630 and

0830. A significant Spearman Rank correlation was found between the number of visits and the number of new egg clutches a male obtained ($r_S = 0.78$, $n = 17$, $p < 0.001$). The number of courtship interactions a male engaged in, however, was not quite significantly correlated to the number of new egg clutches a male received ($r_S = 0.46$, $n = 17$, $p = 0.065$). Male size was not correlated to male reproductive success ($r_S = -0.01$, $n = 14$, $p > 0.05$).

The number of visiting females a male received was significantly correlated with the number of times the male chased other males ($r_S = 0.482$, $n = 17$, $p < 0.05$) and females ($r_S = 0.526$, $n = 17$, $p < 0.05$). Furthermore, a male's aggression towards females, as defined by the number of chases, was positively correlated to the number of new egg clutches he received ($r_S = 0.582$, $n = 17$, $p < 0.05$). Finally, male size was determined to be significantly related to male aggression, towards males and females combined. Smaller males, averaging 2.4 aggressive encounters (SE = 0.46), were found to be more aggressive than large males, who chased an average of 0.4 individuals (SE = 0.08) (Wilcoxon Mann Whitney U Test, $n = 14$, $W_X = 51.5$, $p = 0.03$).

In 11 of 17 female-female encounters observed in the groups, the females ignored one another. The remaining six encounters resulted in aggression, in four of which one female chased the other female who was engaged in courtship. Two aggressive encounters, between two neighboring females in proximity to two reproductively successful males, resulted in mouth fighting.

V. Copying Experiment

An unsuccessful male given a clutch of eggs defended the eggs as if they were his own (66.1% of egg transfers), ate the entire egg clutch (21.4% of egg transfers), or ate a noticeable portion of the egg clutch (12.5% of egg transfers).

Of the males that cannibalized any of the initial clutches of eggs, when given subsequent egg clutches, all eventually would defend them as their own. No male cannibalized clutches after defending eggs given to him. Three males cannibalized two full egg clutches before they defended any eggs given to them. Thirteen other males ate all or part of only one egg clutch before they defended subsequent clutches. In most cases in which the eggs disappeared, the male was actually observed eating the eggs as soon as they were given to him. In less than 25% of the cases, the males were not observed eating the eggs, but cannibalism was assumed to be the cause of the egg disappearance, although predation as a result of the male not defending the eggs properly was possible.

The breeding sites of all males given eggs or an empty tube were inspected the following morning for the addition of new eggs. Twenty-nine percent of the experimental manipulations and 24% of the control switches resulted in the male receiving a new clutch of eggs the following morning, which are not significantly different ($\sum X^2(1) = 0.205$, $p > 0.05$). After the manipulations in which the eggs disappeared were eliminated from the analysis, however, the difference becomes significant ($\sum X^2(1) = 4.2$, $p < 0.05$). Thus, 46.2% of the males who were given eggs and were able to maintain them in the crevice received a new clutch of eggs within one day. Evidence suggests that the presence of eggs increases the probability of receiving a new clutch of eggs for an unsuccessful male, if he does not eat them or allow them to be eaten.

Discussion

Although male and female beaugregory damselfish share the same general habitat, the sexes are not distributed randomly; an individual is more likely to be closer to individuals of the opposite sex. Furthermore, the average female's territory size, as defined by the average furthest distance traveled (see Table 3), clearly overlaps with the primary crevice of her nearest male neighbor (see Table 2). This overlap between territory size and nearest neighbor is less evident between females. Similar distributions have been reported in other polygynous species, often with females having exclusive areas from other females but overlapping with males (Tinkle, 1973; Deslippe and M'Closkey, 1991). The high incidence of aggressive interactions between females in this study and between males reported in other studies (Hoelzer, 1990; Itzkowitz, 1990) suggests that aggression may account for this non-random distribution.

The positive correlation between female size and the number of nearby males suggests two possibilities. First, males may position themselves around larger females. As larger females are expected to have more eggs (Tinkle, 1973; Marconato and Bisazza, 1988; Tejedo, 1992), males may attempt to select localities that allow them to more easily court the larger females. Males do appear to preferentially court larger females and thus, locations closer to large females may be more desirable.

The second plausible explanation accounting for the correlation between female size and the number of nearby males is that large females were able to displace small females. In other studies on fish, larger individuals were capable of usurping the territories of smaller ones (Bisazza et al, 1989) and this may be responsible for the female beaugregory distribution. An advantage gained from more male neighbors is the ability of the female to evaluate more males without

moving long distances. As small and large females maintain the same territory size, smaller females must move greater distances if they are to evaluate the same number of males as do larger females. However, Horne and Itzkowitz (in press) found that larger females courted males at greater distances from their home site than smaller ones. Thus, large females not only position themselves near more males but also travel greater distances to court.

The high incidence of intrasexual aggression between females, especially when one has left her territory, is suggestive of female-female competition for certain locations or mates. In all cases, the resident female was successful in chasing off the intruding female, indicating that the "prior resident effect" is likely more important than size in determining the outcome of such an aggressive encounter. The frequency with which females chased other females courting nearby males suggests that females may, indeed, compete for access to particular males. This type of female-female aggression, where a resident female threatens to attack an intruding female, has been observed in other polygynous territorial species (LaPrade and Graves, 1982). Aggression is clearly a method used by resident females to affect other females attempting to court a nearby male or to settle nearby.

As the beaugregory damselfish breed throughout the year (Itzkowitz, 1985; Robertson, 1990), courtship can be observed at any time and represents the majority (72%) of the behavioral interactions between the sexes. As courtship is considered an evaluative process for mate selection (Schmale, 1981; Bischoff et al, 1985; Kennedy et al, 1987; Knapp and Warner, 1991), I predicted that individuals would direct their courtship behavior non-randomly (i.e., towards preferred mates). The non-random courtship behavior was expected to correlate with the non-random reproductive success of beaugregory

males (Itzkowitz; 1985; Itzkowitz and Makie, 1986; Itzkowitz, 1991; this study). As predicted, larger females were courted more often than smaller ones. This finding coincides with other studies (Côte and Hunte, 1989) in which males selectively court large females and often repel smaller ones. As female size correlates with the number of eggs she carries, male preference for large females is logical. However, as more males are in the vicinity of large females, location alone would account for large females receiving more courtship. Interestingly, individual observations on females revealed no differences in courtship based on female size. However, because the size range of the individually observed females was significantly smaller than the group females, males may court females indiscriminately up to a certain size. When females reach some threshold in size, they may be courted more vigorously.

Females are courted more frequently by larger males than smaller ones. Quite possibly smaller males may experience greater predation pressure and thereby reduce their exposure to predation by courting less frequently. Another possibility is that females prefer larger males and the reduced courtship by small males reflects the reduced likelihood that they will be selected by females. While larger males may engage in more courtship, it may not relate to their reproductive success. For beaugregory males defending artificial breeding sites, male size is not significantly correlated with male reproductive success (Itzkowitz and Makie, 1986). Knapp and Warner (1991) also found no correlation between male size and male reproductive success in the bicolor damselfish, Stegastes partitus. Although the lack of correlation between size and reproductive success could be an artifact of the truncated size range of males inhabiting artificial sites (K. Cole, personal communication), data from this

study indicates no correlation between male reproductive success and size of males occupying natural sites.

The non-random distribution of females and the non-random courtship patterns have the potential to influence the females' mate choices. However, the structure of beaugregory males' spawning sites has been shown to directly affect their reproductive success (Itzkowitz and Makie, 1986; Itzkowitz, 1991). Although a proper control for the manipulation in this study is lacking, previous studies (Itzkowitz, 1991) have shown that males with poor reproductive success will continue to do poorly if the quality of their territory remains unchanged. Thus, we would assume that the resulting interactions between the observed males and females were induced through the addition of the artificial spawning sites. The results suggest that giving a male an artificial spawning site results in new and increased female encounters. This suggests that males may correlate the advertisement of their habitat with the quality of the habitat. Kodric-Brown (1983) observed that male pupfish, Cyprinodon pecosensis, maintaining territories in more preferred habitats, courted more often than did males in less preferred habitats. Studies on other species have indicated that behavior is a truthful advertisement of an individual's quality (Rohwer and Rohwer, 1978). This phenomenon may account for smaller males courting less than larger males and males with better quality habitats courting more than males with poorer quality habitats.

Females may also be influenced by where other females have already spawned. This phenomenon, termed "copying," occurs when females prefer to mate with males that were previously selected by other females (Ridley and Rechten, 1981; Gronell, 1989; Hoelzer, 1990). Beaugregory females do appear to copy other females, since males that were given eggs from other males

received significantly more egg clutches, as long as they do not eat them, than males not given eggs. As clutch size is significantly correlated to egg survival in the beaugregory damselfish (Itzkowitz and Makie, 1986), as in other species (Bisazza and Marconato, 1988; Gronell, 1989; Goldschmidt et al, 1993), females may benefit by having their eggs as part of a larger mass of eggs to reduce the probability of clutch loss through predation or filial cannibalism. It is also possible that females may evaluate a male's ability to raise and protect eggs by the presence of other egg clutches.

The process of copying requires that females evaluate males and/or male spawning sites. Females could use the heightened aggression seen in males defending eggs (Itzkowitz, 1990) as an indicator for the presence of eggs. Quite possibly females are courted more by males who are caring for eggs. Alternatively, females may inspect the male's spawning site, through visiting, for the presence of eggs. Goldschmidt et al (1993) found that female three-spined sticklebacks showed no preference for males with eggs when they were not permitted access to the nests, suggesting that females must observe the eggs to become aware of their presence. This finding is supported by evidence in this study and a previous study (Hoelzer, 1990) indicating that females enter many nest sites without spawning, although data from the present study also found that males receiving more visiting females obtained more spawnings.

Finally, females visited and spawned with males that chased females more often, suggesting two possibilities. First, females may eat eggs in the nest. Increased aggression towards females may be a strategy by males to single out females that are most interested in spawning and will tolerate the males' aggression. Alternatively, females may use the heightened aggression level

found in males defending eggs (Itzkowitz, 1990) as a measure of the males' ability to defend their broods.

In conclusion, beaugregory damselfish females are capable of assessing many males before choosing to mate. In reference to Janetos' models (1980), females are not mating randomly (model 1) or using the threshold model (model 2; i.e., they do reassess and mate with previously rejected males once their habitat quality improves). Females continually visit many males, suggesting a "one-step decision" process or the "best-of-N" strategy. As large females do interfere with the distribution and courtship of smaller females, any model of the assessment process must account for this interference. Data from the beaugregory damselfish also suggests that males preferentially court larger females suggesting that both sexes are involved in the mate selection process.

Test variable	Males	Females
Courtship	0.54	Including unidentified females: 0.75
		Without unidentified females: 2.57
Number of visiting events	0.54	Including unidentified females: 0.93
		Without unidentified females: 3.43
Size (TL)	2.17	2.2
Size (FL)	2.17	1.92
Aggression against males	AM: 0.11	Combined AM + PM: 0.16
	PM: 0.30	
Aggression against females	AM: 2.51	AM: 2.12
	PM: 0.35	No PM aggression

Table 1. Kruskal Wallace Test values for the three groups of males and females from the "Group Observations". For all tests, $p > 0.05$.

	Male-Male	Male-Female	Female-Female	Female-Male
N	14	13	21	21
Mean (m)	1.62	1.33	1.72	1.31
SE	0.097	0.085	0.114	0.078
p Value	p = 0.03		p = 0.01	

Table 2. Nearest neighbor distances between males and females. Wilcoxon Mann Whitney U Tests indicate that males are distributed significantly closer to females and females are significantly closer to males (one-tailed tests).

	Average (SE)	Furthest Overall (SE)	Average Furthest (SE)
AM	0.69 (.125)	3.09 (.726)	1.85 (.227)
PM	0.59 (.125)	2.3 (.325)	2.02 (.338)
Combined AM + PM	0.65 (.093)	3.07 (.593)	1.87 (.221)

Table 3. Average distances (m) traveled from primary crevices by individual females ($n = 14$). Wilcoxon Signed Ranks Tests determine that the "Furthest Overall" distances traveled by females is significantly different in AM vs. PM ($p = 0.02$). "Average" distances and "Average Furthest" distances are not significantly different in AM vs. PM ($p > 0.05$).

	# Events/15 minutes	Standard Error	% of F/M Interactions
Total F/M Interactons	2.21	0.4	100%
Courtship	1.59	0.332	71.90%
Visiting	0.054	0.02	2.40%
Mating	0.005	0.005	0.23%
Female chases Male	0.158	0.043	7.15%
Male chases Female	0.218	0.067	9.86%
Ignore each other	0.187	0.052	8.46%

Table 4. Results of female-male (F/M) interactions taken from individual female observations (N = 14).

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Vitae

April Dawn Renshaw, the daughter of Francis and Shirley Renshaw, was born on June 27, 1969, in Stratford, New Jersey. She graduated from Overbrook Regional High School in 1987, where she was a member of the National Honor Society. In 1991, April received her Bachelor of Science in Marine Biology from the Richard Stockton College of New Jersey. While attending Stockton, she was selected twice for the College Scholar Award, based on her academic achievement. She graduated with Highest Honors and Program Distinction.

April has dedicated her time and efforts continually through volunteer work and employment in her field. She served for several years as a volunteer for the Marine Mammal Stranding Center in Brigantine, New Jersey, where she aided in the recovery of injured marine animals. She worked on a fishing vessel in the Bering Sea for three months, where she collected fisheries data for the National Marine Fisheries Service. April also worked as a field assistant for the New Jersey Division of Fish, Game, and Wildlife. There, she performed studies on the evaluation of the population status of fish and shellfish of the Delaware Bay using research and survey techniques. Prior to pursuit of her Master's degree at Lehigh University, April was employed by the University of Delaware, College of Marine Studies, where she initiated a tagging study on a commercially important fish species and aided in other fisheries-related research. While at Lehigh University, April contributed as a teaching assistant for biology-related lab and field courses.

Upon completion of her Master's degree in biology, April intends to pursue a career in environmental protection and research.

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